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THE FROGS OF THE GENUS *ELEUTHERODACTYLUS* (FAMILY LEPTODACTYLIDAE) AT THE LA PLANADA RESERVE IN SOUTHWESTERN COLOMBIA WITH DESCRIPTIONS OF EIGHT NEW SPECIES

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As presently constituted, the genus *Eleutherodactylus* is the largest genus of vertebrates recognized with more than 430 species distributed from Texas and the Bahamas to Argentina. It becomes even larger if the 25 or so species of the genera *Sminthillus*, *Syrrhophus*, and *Tomodactylus* are included as recommended by Hedges (1989). There are places, in very humid lowland forests, at which one can find 15–20 species living more or less sympatrically (Lynch, 1979, 1980a) whereas in upland areas one rarely finds more than 6–10 species. The richness of the genus *Eleutherodactylus* is only partially attributable to its ecological diversification (few studies have demonstrated food or habitat specialization within communities and then only for a few species).

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The bulk of the species density of *Eleutherodactylus* is accounted for as a geographic phenomenon where species "replace" one another along a geographic gradient. Such geographic replacement appears to be most acute at moderate altitudes rather than in the lowlands or in the very high altitude habitats (Lynch, 1987).

The fauna which we describe here was sampled by the junior author during a 3 month field study (April–June 1986). It had been expected that the La Planada fauna (Cordillera Occidental, Departamento Nariño) would be a mixture of those from a series of sites slightly to the north (Cerro Munchique region, Departamento Cauca, Colombia) and those to the south (several studied sites in Provincias Carchi [Maldonado], Imbabura [Las Delicias], and Pichincha [Tandapi]). However, the La Planada site is of interest for two reasons. Firstly, although some previously known species of restricted distributions were found, 42% of the species (eight described here as new) from La Planada appear to be species not previously found. Secondly, the size of the eleutherodactyline frog fauna is surprising. The junior author collected at essentially 2 altitudes within the reserve. One of these is near the lower limit of the park (1250 m) whereas the other is on the plateau forming most of the park (1750–1780 m). Two species were found only at the lower elevation but on the plateau she found 17 species of *Eleutherodactylus*. With only 3 months of field work, we are reluctant to suggest that all species of *Eleutherodactylus* living at this cloud forest site have been found. However, we are skeptical that the fauna might be larger than 19 species. We remain impressed by the La Planada eleutherodactyline fauna especially by way of contrast to Duellman's (1978) finding of a mere 16 species in 48 man-months of field work in Amazonian Ecuador. Using subjective a posteriori abundance categories, the newly discovered species represent a cross-section of the eleutherodactyline frog fauna (Table 1) and do not reflect disproportionately the rarest end of the abundance spectrum. Two of the most common eleutherodactyline frogs at La Planada are described herein.

GENERAL HABITAT

La Reserva Natural La Planada is a 1667 ha^2 tract occupying primarily a forested plateau (Very Humid Premontane Tropical Forest of Holdridge, 1967) at 1780 m. The altitudinal limits of the reserve are 1200 and 2100 m. The plateau is drained by many cold (18°C), clear streams flowing over sand, gravels, and rock. The streams eventually empty into the Rio Guiza or the Rio Nulpe which in turn enter the Rio Mira.

Based on data (from 1985–86) provided by G. Cantillo, the estimated annual precipitation at La Planada is 5000 mm. During the 3 months of field work (April–June 1986), the average daily temperature varied from 13.1 (night time low) to 22.8°C (noon). At mid-afternoon, when dense low clouds

Table 1. Ecological summary of the *Eleutherodactylus* species of the La Planada Reserve. New species are marked with an asterisk.

Species	Abundance[1]	Activity	General habitat
E. achatinus	1	nocturnal	Pastures, forest edge
E. anatipes	4	nocturnal	Streams, cascadas
*E. apiculatus**	1	nocturnal	Forests
E. appendiculatus	5	diurnal(?)[2]	Forests
*E. babax**	3	nocturnal	Terrestrial, forests
E. celator	3	nocturnal	Forests, bromeliads
E. duellmani	2	nocturnal	Streams, cascadas
E. eremitus	4	nocturnal	Forests
*E. hectus**	1	diurnal	Terrestrial, forests
*E. laticlavius**	3	nocturnal	Forested streams
E. loustes	5	nocturnal	Streams, cascadas
*E. ocellatus**	5	nocturnal	Forested streams
E. quinquagesimus	2	nocturnal	Forests
*E. scolodiscus**	3	nocturnal	Forests
*E. siopelus**	3	nocturnal	Forested streams
*E. sulculus**	5	nocturnal	Forested streams
*E. verecundus**	3	nocturnal	Forested streams
E. w-nigrum	2	nocturnal	Forested streams

[1]Subjective abundance rating from 1 (= very common) to 5 (= rare)
[2]See text

covered the sky, the temperature would drop abruptly to about 18°C. During the field study, measurable rain fell on all but 5 days; typically, rain began at approximately 1600 h and continued through the night. Average daily precipitation was 15 mm.

Most of the native forests at La Planada are intact. There is some damage evident from previous clearings for pasture and some trails cut for commercial timber exploitation. Forest trees have a maximum observed height of 25 m and are covered by epiphytic plants (Araceae, Bromeliaceae, and Orchidaceae). The tree canopy is dense and allows little penetration of light. The understory and ground vegetation of saplings, tree ferns, and herbaceous plants is moderately dense. The forest floor is permanently covered by leaf litter and fallen tree branches (or trunks) colonized by a diversity of fungi, lichens, and mosses.

MATERIALS AND METHODS

The format and conventions of the descriptions which follow are those used by Lynch and Duellman (1980). Abbreviations used in the text are as follows: E–N (eye to nostril distance), HW (greatest width of head), IOD (interorbital distance), and SVL (snout–vent length). When means are re-

ported, they are reported as mean ± one standard error. Unless stated otherwise, measurements are of adult frogs (maturity having been established by examination of gonads). Specimens are identified in the text using an abbreviation for the museum collection, as follows: ICN, Instituto de Ciencias Naturales, Bogotá; IND-AN, amphibian collection, Instituto Nacional de los Recursos Naturales Renovables y del Ambiente, Bogotá; KU, Museum of Natural History, The University of Kansas. Specimens identified with the prefix PAB are deposited in a reference collection at the Reserva Biologica "La Planada."

SPECIES ACCOUNTS

Eleven species found by the junior author are species previously known. For these taxa, we report the local records and provide a miscellany of observations.

Eleutherodactylus achatinus (Boulenger)

This was the only species of *Eleutherodactylus* found in *potreros*. In addition to being common in pastures, these frogs were found on vegetation (at night) along the roadside leading into the reserve. Adults were seen sitting on leaves of bushes (up to 50 cm above the ground) and in bunch grasses. Bursts of activity (frogs moving about, calling males) were correlated with extremely dark, foggy nights. No other eleutherodactyline species was sympatric (ecologically) with *E. achatinus*. The only color pattern evident in our samples is the *achatinus* morph (see Lynch and Myers, 1983).

Eleutherodactylus anatipes Lynch and Myers

This species was found at sites lying at the lower limit of the reserve (1200–1250 m). Only juvenile individuals (Fig. 1A) were found. The frogs were active at night, sitting on rocks or in rocky crevices alongside large streams, or on very steep rock cliffs constantly washed by runoff. The surrounding habitat was disturbed (the forests had been cut to provide clearings for the cultivation of plantane and sugar cane). In 1982, Pedro M. Ruiz secured one specimen (ICN 12113) from La Planada at a slightly higher elevation (1600 m).

Eleutherodactylus appendiculatus (Werner)

Although not reported previously from Colombia, the presence of this species is not surprising. Only five individuals were collected, all within a

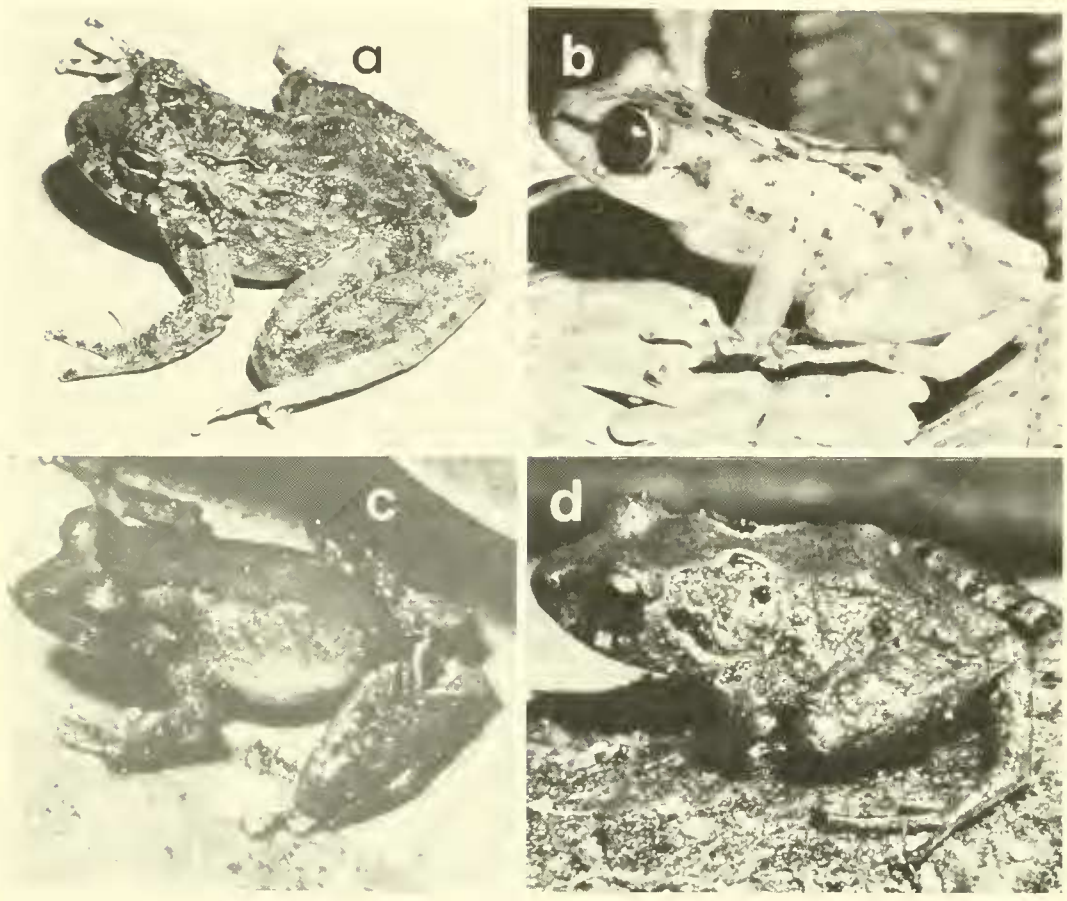

Fig. 1. *Eleutherodactylus* from La Planada. A) *E. anatipes*, PAB 568, juvenile; B) *E. eremitus*, PAB 399, sex not known, adult; C) *E. apiculatus*, IND-AN 1755, adult female, 21.6 mm SVL; and D) *E. hectus*, IND-AN 1957, adult female, 21.0 mm SVL.

small stretch of a single trail at about 2000 m. The frogs were found by day and were actively hopping about in vegetation some 1.5 m above the ground in dense forest. These observations are quite dissimilar to the ecological notes provided by Miyata (1980) for the species in Ecuador. These frogs appear to be immature (no vocal slits) but differ in at least one feature from samples from Pichincha, Ecuador, in that the lining of the testis is heavily flecked with melanophores (lightly flecked or not flecked in Ecuadorian specimens).

Eleutherodactylus babax Lynch

This is a species of the *discoidalis* group of Lynch (1976a) and was described in a review of that "group" by Lynch (1989) who included *E. babax* and *E. dolops* in a *dolops* group. As is the case for all members of the *discoidalis* "group," this species is terrestrial. Frogs were active on the forest floor or on mud banks of streams at night. The species was recognized easily at night because individuals have a bright orange-red eyeshine.

This species is most similar to *E. dolops* Lynch and Duellman but does not

grow to be so large (males to 42.4 mm SVL, one adult female 48.7 mm SVL). A male secured in November 1982 (ICN 13592) was calling during a heavy rain.

Eleutherodactylus celator Lynch

Previously, this species had been collected by day from arboreal and terrestrial bromeliads in the provinces of Carchi and Imbabura of Ecuador at elevations of 2500–2700 m. At La Planada, this species was also found in arboreal bromeliads by day. At night, individuals of *E. celator* were found on leaves and mossy branches 1.0–2.5 m above the forest floor. Because the trees at La Planada are densely covered with epiphytes, the frogs were never very far from bromeliads but no clear association was evident.

Eleutherodactylus chalceus (Peters)

This species was abundant in forests at night where it was found on leaves and mossy branches. Males were observed calling every night during the 3 month study by the junior author.

Eleutherodactylus duellmani Lynch

This species was previously reported from Colombia by Lynch and Ruiz (1983) from Depto. Cauca and was expected to be found in Depto. Nariño. Individuals were found inside crevices or on rocks in small streams at night. Many of the individuals observed by the junior author were found under small water falls.

Eleutherodactylus eremitus Lynch

This species had not been reported from Colombia previously and had been known from relatively few specimens from Provincia Pichincha, Ecuador (Lynch, 1980b). Seven individuals were secured at La Planada. This uncommon frog (Fig. 1B) was found sitting at night on broad leaves, ferns, or mossy tree branches. One specimen (IND-AN 1487) was obtained at night from an observation tower: the frog was sitting on a leaf (Guttiferaceae) approximately 7.0 m above the ground. Some individuals were found by day in arboreal bromelias.

Because the species is uncommon, we provide the following color notes: dorsum green with reddish-brown markings (loose reticulation or flecking) over body and a reddish-brown blotch on head; venter creamy white; iris copper with fine black reticulations. One individual (IND-AN 1487) had an orange-yellow dorsum with broad reddish-brown dorsolateral bands; flanks

brown; limbs orange-tan with brown transverse bars; venter yellow with an orange suffusion over limbs. A similar range of color pattern variation was noted in the original description (Lynch, 1980b:5 and Fig. 2). In the original description, *E. eremitus* was noted as having "colorless areas in groin and on posterior surfaces of thighs." In our specimens, there is some dark stippling providing definition to the pale spots in the groin and on the posterior surfaces of the thighs. We are not able at this time to decide if this represents geographic or individual variation.

Eleutherodactylus loustes Lynch

Only two individuals were found of this species but they provide the first record of the species from Colombia (although the type-locality lies virtually on the Colombia–Ecuador frontier). *Eleutherodactylus loustes* was found at San Isidro (1200 m) at the lower limit of the reserve. The frogs were found sitting on rocks in a stream and on very steep mud banks under the water falls.

Eleutherodactylus quinquagesimus Lynch and Trueb

This species is reported from Colombia for the first time being previously known from Provincias Imbabura and Pichincha of Ecuador (Lynch and Trueb, 1980). Structurally, the samples from La Planada do not differ from those known previously. These frogs are from lower elevations than those from Ecuador. Specimens were active at night on vegetation within the forest some 1.0–2.5 m above the ground. Individuals were also found along stream banks.

Lynch and Trueb (1980) reported geographic variation in this species and we add to its known geographic variation. At La Planada, adult males are 20.3–24.6 mm SVL ($\bar{x} = 23.2 \pm 2$, $n = 17$) and adult females are 30.5–34.0 mm SVL ($\bar{x} = 32.3 \pm 0.4$, $n = 9$). Lynch and Trueb (1980) reported much larger frogs from Ecuador (males 27.8–30.8 mm SVL [$\bar{x} = 28.9$], females 33.6–40.1 mm SVL [$\bar{x} = 35.8$]). Ratios were computed for adult females and are as follows (expressed as percents): Tibia/SVL 59.4–68.5 ($\bar{x} = 61.7 \pm 0.9$), HW/SVL 40.5–45.9 ($\bar{x} = 42.5 \pm 0.5$), eyelid width/IOD 82.0–113.3 ($\bar{x} = 94.0 \pm 3.5$), E–N/eye 85.4–109.8 ($\bar{x} = 97.4 \pm 3.1$), and tympanum/eye 17.0–29.3 ($\bar{x} = 23.1 \pm 1.2$) [$n = 9$ in each case].

These proportions demonstrate some differences between Colombian and Ecuadorian samples.

The coloration of the frogs from La Planada is as follows: dorsum chocolate-brown or reddish-brown with (or without) darker brown-black markings consisting of chevrons, blotches, interorbital bars, and transverse limb bars; flanks brown with varying degrees of white mottling; venter white with brown flecks (usually most concentrated on throat); throat bearing dark inverted

chevrons; upper lip and inner two fingers white; iris brown with a gold rim around orbit. In several individuals, the flanks are brown with orange flecks forming diagonal lines to the venter.

We take this opportunity to report another locality for *E. quinquagesimus* (KU 179391, Ecuador, Prov. Carchi, Maldonado, 1410 m); this is the lowest altitudinal record available.

Eleutherodactylus w-nigrum (Boettger)

Adults were found sitting on low vegetation (0.2–0.5 m above ground) in the forest at night. Juveniles were active on the forest floor and along forested stream banks during the day. Occasionally, juveniles were found sleeping on leaves of low vegetation at night.

THE NEW SPECIES

The eight species which we describe as new include seven which would fall in Lynch's (1976a) *unistrigatus* series and one which fits awkwardly between the *fitzingeri* and *unistrigatus* series. Each exhibits condition "S" of the *m. adductor mandibulae* (Lynch, 1986). In the following descriptions, when the condition/morphology is sufficiently described in the numbered statements of the diagnosis, the material is not repeated in the description. Each of the new species, as well as all previously described except for *E. anatipes*, is a member of what Hedges (1989) has designated as the subgenus *Eleutherodactylus*. The only exception is a member of the subgenus *Craugastor* (Hedges, 1989; Lynch, 1986).

Eleutherodactylus apiculatus, New Species

Fig. 1C

Holotype.—IND-AN 1506, an adult female, one of a series collected at Reserva Natural La Planada, 7 km S Chucunez, Mcpio. Ricaurte, Depto. Nariño, Colombia, 1780 m, on 12 June 1986 by P. A. Burrowes.

Paratypes.—IND-AN 1448–49, 1451–52, 1454–55, 1499–505, 1507–09, 1552, 1744–46, 1749–51, 1754–74, 1776, 1780, 1782–83, 1787–88, 1791, 1802–03, 1806–07, 1824, KU 212534–38, and PAB 172, topotypes.

Diagnosis.—1) skin of dorsum essentially smooth, no dorsolateral folds, that of venter areolate; 2) tympanum distinct, 24–38% eye length, slightly larger in females than in males; 3) snout subacuminate in dorsal view, subtruncate in lateral profile; canthus rostralis evident; 4) upper eyelid narrower than IOD, bearing one non-pungent tubercle; no cranial crests; 5) vomerine odontophores oval to slanted, not prominent; 6) males with vocal slits; 7) first

finger shorter than second; pads and discs on all fingers, largest on outer fingers; 8) fingers with narrow lateral fringes; 9) no ulnar tubercles; 10) small tubercle on heel; outer edge of tarsus bearing row of low tubercles; 11) two metatarsal tubercles, inner oval, 3 times size of elongate outer; many low supernumerary plantar tubercles; 12) toes with lateral fringes, no webbing; toe pads larger than those of fingers; 13) color pattern polymorphic; most common pattern is brown dorsum with pale interorbital bar and cream line above dark anal patch, venter paler brown (darkest on throat); concealed surfaces of limbs and groin brown; 14) adults small, males 17.8–21.8 mm SVL ($\bar{x}$ = 20.3 ± 0.2, n = 24), females 21.6–26.3 mm SVL ($\bar{x}$ = 23.3 ± 0.3, n = 17).

Eleutherodactylus apiculatus is most similar to (and presumably most closely related to) *E. boulengeri* Lynch and *E. calcarulatus* Lynch but is obviously smaller than either of those species. In addition, *E. calcarulatus* has a distinct conical tubercle on the heel (small, non-conical tubercle in the other two), small ulnar tubercles, and an inner tarsal tubercle. *Eleutherodactylus boulengeri* also differs from *E. apiculatus* in having ulnar tubercles but also differs in having low cranial crests in females and in having nuptial pads in males. The calls of *E. apiculatus* (two notes) and *E. boulengeri* (one note) differ but the call of *E. calcarulatus* remains unknown to us. These three species have similar distributions of color morphs.

Description.—Head as wide as body, wider than long; HW 35.7–39.7% SVL ($\bar{x}$ = 37.9 ± 0.3) in males, 34.4–41.9% ($\bar{x}$ = 37.8 ± 0.7) in females; in lateral profile snout subtruncate or rounded, bearing papilla at tip; snout long; E–N 71.4–90.0% eye length ($\bar{x}$ = 80.2 ± 2.0) in males, 82.9–93.9% ($\bar{x}$ = 88.2 ± 1.1) in females; nostrils not or only weakly protuberant, directed dorsolaterally; canthus rostralis evident (edge is rounded), slightly concave; loreal region concave, sloping abruptly to lips; lips not flared; upper eyelid width 57.7–92.0% IOD ($\bar{x}$ = 77.4 ± 3.6) in males, 80.0–108.0% ($\bar{x}$ = 90.0 ± 3.0) in females; upper eyelid bearing small, insignificant tubercles but under magnification one flat tubercle is evident on posterior portion of upper eyelid; supratympanic fold low, ending in series of small warts; tympanum prominent, directed posterolaterally, round, separated from eye by distance about equal to its own diameter; tympanum length 24.2–35.3% eye length ($\bar{x}$ = 30.4 ± 1.1) in males, 29.4–38.2% ($\bar{x}$ = 33.4 ± 0.9) in females; postrictal tubercles subconical; skin of head relatively smooth, some low tubercles evident in temporal region; choanae moderate-sized, not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly below; vomerine odonotophores medial and posterior to choanae, each about size of a choana, oval or somewhat slanted, relatively low, bearing slanted row of 5–6 teeth; odontophores separated on midline by distance slightly greater than width of an odontophore; tongue longer than wide, posterior edge notched, posterior ⅖ not adherent to floor of mouth; long vocal slits posterolateral to tongue in

males; vocal sac subgular.

Skin of upper surfaces smooth except for some granulation on flanks; anal opening not extended in sheath; discoidal folds well anteriad to groin; palmar tubercle bifid, much larger than oval thenar tubercle; numerous supernumerary palmar tubercles; subarticular tubercles round; narrow fleshy fringes on lateral margins of fingers; pad on thumb scarcely expanded, those on fingers III and IV as wide as tympanum; pads and discs broader than long; pads rounded apically; males lacking nuptial pads.

Inner margin of tarsus lacking tubercles; many low supernumerary plantar tubercles, larger ones at bases of toes II, III, and IV; subarticular tubercles round; large digital pads on toes; when hind legs are flexed at right angles to sagittal plane, heels overlap broadly; heel of adpressed hind limb reaches to between eye and nostril; shank 50.0–55.1% SVL ($\bar{x} = 52.7 \pm 0.6$) in males, 50.6–59.0% ($\bar{x} = 54.1 \pm 0.8$) in females.

Coloration in preservative: dorsal surfaces brown with faint indication of darker markings (oblique limb bars, narrower than interspaces); pale interorbital bar present; dark anal triangle present, delimited by cream line; tympanum generally lighter than adjacent skin; often ill-defined cream patch below eye; labial bars and canthal-supratympanic stripe indistinct or absent; venter more pale than dorsum, cream stippled with brown, most intense on throat; groin, anterior and posterior surfaces of thighs, and concealed surfaces of shank brown. (Also see Remarks section for variation in color patterns).

In life, *E. apiculatus* is brown, tan, or yellowish-tan above with a black interorbital bar and with (or without) small brown blotches of varying shape; limbs tan with brown bars; venter white or yellow with brown flecking; anal triangle dark brown bordered anteriorly by yellowish-tan line; concealed surfaces of limbs brown; iris bronze with a median reddish-brown streak and black reticulation. Some individuals (IND-AN 1791, 1802, KU 212538) are brown dorsally with a wide yellow-tan middorsal stripe and yellow-tan blotches on the heels and elbows. In others (IND-AN 1771–72, 1807) the dorsum has many fine yellow stripes on a brown background.

Measurements of holotype in mm.—SVL 23.5; tibia 12.7; HW 8.5; head length 9.5; upper eyelid width 2.6; IOD 2.1; tympanum 1.1; eye length 3.0; E–N 2.7.

Etymology.—The trivial name is Latin, meaning small or pointed and is used in reference to the small heel tubercle.

Natural history.—This species was very abundant in the forest at night. Calling males ("peeep-peeep") and gravid females were encountered throughout the study period. Adults were found sitting on leaves, fronds, and mossy tree branches 1.0–3.5 m above the forest floor.

Remarks.—As is the case for many species of *Eleutherodactylus*, *E. apiculatus* is pattern polymorphic. The most common pattern is that described above (coloration in preservative). This morph, *brown frog with pale interor-*

bital bar, is found in 41 of 67 individuals (38 were sexed, 18 males and 20 females). The next most abundant morph, *many thin dorsal lines*, is seen in nine individuals (five males and four females). The only morph sexually restricted is one with *dark hour-glass mark on back* (the anterior edge of the dark mark is defined by the pale interorbital bar; laterally, the mark is defined by broad dorsolateral stripes which fade out at about the level of the sacrum). This morph is found only in eight females. The *narrow dorsolateral stripes* morph is seen in four individuals (two males, two females). The *broad pale vertebral band* morph (with pale patches on the elbows and heels) is seen in four individuals (three males and one female). One other morph is represented by a single female individual (a morph in which the frog is brown with a large cream blotch on top of the head).

The largest juvenile male (no vocal slits) is 18.2 mm and overlaps the size range of adult males. The largest juvenile females (straight, thin oviducts, small ovarian eggs) are 21.2 and 21.6 mm SVL. Young females (showing convolutions of the oviducts but with small eggs) are 21.5–21.6 mm SVL.

Eleutherodactylus apiculatus is probably most closely related to *E. calcarulatus* which shares with it a similar distribution of pattern polymorphs (see Lynch, 1976b:8–9). One should not use pattern polymorphism as a systematic character until the character is better understood. For example, an equally good case might be made to associate *E. variabilis* with *E. apiculatus* based on pattern polymorphism (see Lynch, 1968) but that species shares few other traits with these cloud forest denizens.

Eleutherodactylus hectus, New Species

Figs. 1D, 2A

Holotype.—IND-AN 1947, an adult female, one of a series collected at Reserva Natural La Planada, Mcpio. de Ricaurte, Depto. Nariño, Colombia, 1780 m, on 23 April 1986 by P. A. Burrowes.

Paratypes.—IND-AN 1456, 1513–14, 1920–24, 1926, 1928–31, 1933–37, 1940–46, 1949–57, 1959–60, KU 212539–544, topotypes.

Diagnosis.—1) skin of dorsum granular to tuberculate, that of venter areolate; prominent dorsolateral folds; 2) tympanum prominent, round in males, higher than long in females, its length 43–54% eye length in males, 27–46% eye length in females; 3) snout subacuminate in dorsal view, rounded in lateral profile; canthus rostralis sharp; 4) upper eyelid narrower than IOD; no cranial crests; upper eyelid tuberculate, bearing 2–3 subconical tubercles; 5) vomerine odontophores oval; 6) males with short vocal slits, lacking nuptial pads; 7) first finger shorter than second; discs on fingers II–IV, pads dilated, small; 8) lateral keels on fingers; 9) row of ulnar tubercles, antebrachial largest; 10) small tubercles on heel, row of larger tubercles along outer edge of tarsus; short fold-like tubercle on inner edge of tarsus; 11) two

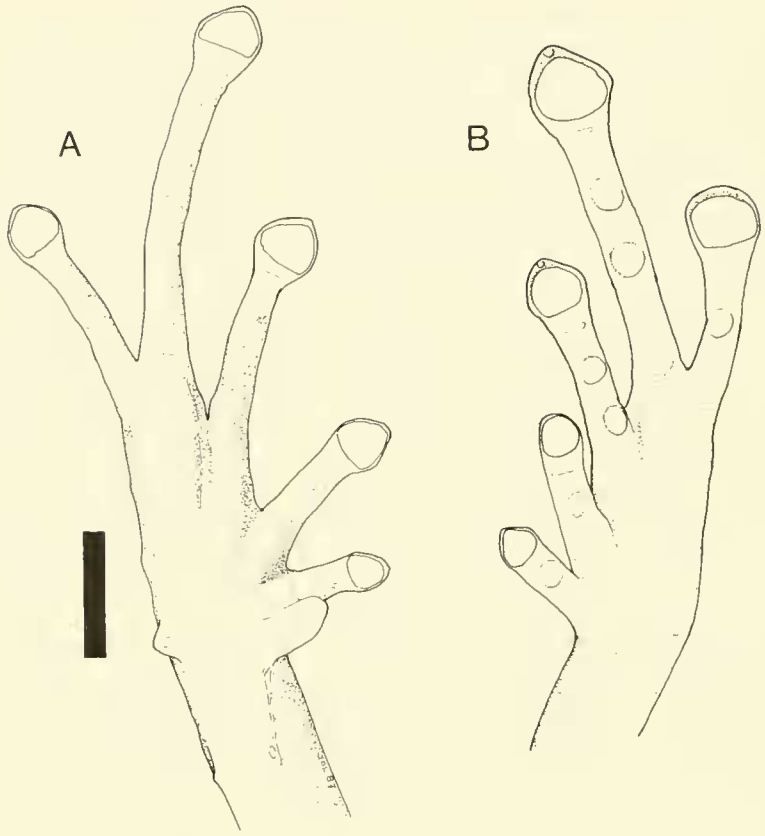

Fig. 2. Plantar views of feet of A) *Eleutherodactylus hectus*, IND-AN 1941, and B) *E. scolodiscus*, IND-AN 1473. Scale equals 2 mm.

metatarsal tubercles, inner oval with distal end free, 4 times size of subconical outer metatarsal tubercle; 12) toes bearing narrow lateral keels and expanded, lanceolate digital pads; 13) dorsum gray or brown with dark brown markings (canthal stripe, labial bars, and dorsal spotting), venter pale brown with vague brown blotching; groin and posterior surfaces of thighs brown with (or without) cream spots; 14) adults small, males 13.6–16.8 mm SVL ($\bar{x}$ = 15.2 ± 0.2, n = 13), females 19.4–22.5 mm SVL ($\bar{x}$ = 20.7 ± 0.2, n = 20).

Eleutherodactylus hectus closely resembles *E. leoni* and *E. pyrrhomerus* but does not appear to be a member of that species group because it has larger digital pads than does any member of that group, all of which also have red or orange flash colors (Lynch, 1984). We are reluctant to associate *E. hectus* with any other species group. It is most easily distinguished from other species by virtue of its peculiar inner metatarsal tubercle (Fig. 2) but can also be distinguished in the possession of lanceolate pads on the toes, a feature which appears in few other species of the genus. *Eleutherodactylus hectus* may prove to be allied to such species as *E. leptoloplus* Lynch and *E. peraticus* Lynch but is easily distinguished from them based on digital morphology and skin texture.

Description.—Head nearly so wide as body, wider than long; HW 36.9–44.1% SVL ($\bar{x}$ = 40.8 ± 0.8, n = 10) in males, 38.7–43.1% ($\bar{x}$ = 41.2 ±

0.4, $n = 10$) in females; papilla at snout tip; nostrils slightly protuberant, directed laterally; snout short, E–N 56.0–68.2% eye length ($\bar{x} = 64.4 \pm 1.4$, $n = 10$) in males, 68.8–83.3% ($\bar{x} = 75.3 \pm 1.7$, $n = 10$) in females; canthus rostralis weakly concave; loreal concave, sloping abruptly to lips; lips not flared; upper eyelid tuberculate, 2–3 larger subconical tubercles evident, largest posterior on eyelid; upper eyelid width 72.2–108.3% IOD ($\bar{x} = 92.9 \pm 4.6$, $n = 10$) in males, 75.0–104.3% ($\bar{x} = 90.5 \pm 2.4$, $n = 10$) in females; supratympanic fold thin; tympanum higher than long in females, larger and round in males (separated from eye by its own length in females but by a distance only ½ to ⅔ tympanum length in males); tympanum length 43.5–54.6% eye length ($\bar{x} = 48.0 \pm 1.1$, $n = 10$) in males, 26.7–46.2% ($\bar{x} = 37.0 \pm 1.9$, $n = 10$) in females; postrictal tubercles large, conical; choanae small, not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly above; vomerine odontophores median and posterior to choanae, each larger than a choana, separated on midline by a distance about equal an odontophore width; tongue longer than wide, posterior edge bearing notch, posterior ⅖ not adherent to floor of mouth; males with short vocal slits posterolateral to tongue and subgular vocal sac.

Skin of head tuberculate, some tubercles fusing to form short ridges; occipital W formed by tubercles and ridges in most individuals; skin on face tuberculate, especially anterior to tympanum; skin of dorsum granular, becoming tuberculate laterally; in most individuals there is a pair of dorsolateral folds with little indication of other folds but in other individuals, there are several vertebral and paravertebral folds lying between the doroslateral folds; flanks tuberculate; anal opening not extended in sheath; discoidal folds just anteriad to groin; upper surfaces of limbs tuberculate.

Three ulnar tubercles, antebrachial largest; palmar tubercle bifid (or divided into two), larger than oval thenar tubercle; many small supernumerary palmar tubercles; subarticular tubercles low, round; no disc on thumb, its pad scarcely dilated, pointed; pad of second finger dilated, pointed in many individuals, rounded in others; pads of fingers III–IV clearly larger, usually rounded apically, none so large as tympanum, even in females.

Small tubercles on heel (none especially prominent) with larger, more pungent tubercles along outer edge of tarsus; short, fold-like tubercle on inner edge of tarsus, not attached to inner metatarsal tubercle; inner metatarsal tubercle oval, displaced medially so that distal end is free (Fig. 2A); plantar surface with many minute supernumerary tubercles; subarticular tubercles round; all toes bear discs on ventral surfaces of lanceolate pads; when hind limbs are flexed at right angles to sagittal plane, heels touch or overlap only slightly; heel of adpressed hind limb reaches to between eye and nostril; shank 46.4–58.1% SVL ($\bar{x} = 53.1 \pm 1.3$, $n = 10$) in males, 47.7–53.0% ($\bar{x} = 50.9 \pm 0.6$) in females.

Coloration in preservative: gray, pale brown, or darker brown above with

dark brown canthal-supratympanic stripe and labial bars; other dorsal markings include interorbital bar, heavy scapular chevron, sacral chevron, and suprainguinal spots; limb bars on shank narrower than interspaces, oblique; anal triangle edged above by cream line; groin, anterior and posterior surfaces of thighs brown, spotted or not with cream; ventral surfaces pale brown with vague brown blotching, darkest blotches at edges of lower lips (coincidental with labial bars); flanks blotched.

A less common color pattern is the *dorsoconcolor* pattern. This pattern is coincidental with the presence of heavy dorsolateral folds and consists of a creamy-brown dorsum without markings bordered laterally by dark flanks. The common color pattern can have superimposed upon it a pale hairline vertebral stripe or a pale interorbital bar and pale urostylar band.

In life, *E. hectus* is usually brown, tan, or reddish-brown above with creamy-white, black, or brown markings. Some individuals (IND-AN 1920, 1960, KU 212541) have a dark brown middorsal line and prominent dark brown dorsolateral lines. In IND-AN 1952 there is a creamy-white middorsal line but the dorsolateral lines are not distinct. An orange-tan blotch on the head or a black interorbital bar is present in most individuals. The limbs are usually brown or tan with darker brown or black transverse bars. The groin and hidden surfaces of the limbs are brown with white flecks (or clumped into spots). The flanks are brown with varying degrees of creamy-white mottling. The venter is yellow-tan with brown flecks or is brown with creamy-white specks. The iris may appear to be dull brown to greenish or bluish-bronze with a red median stripe. These variations probably reflect the light available when field notes were taken rather than individual variation.

Measurements of holotype in mm.—SVL 20.9; tibia 10.7; HW 9.0; head length 8.4; upper eyelid width 2.0; IOD 2.3; tympanum length 1.0; eye length 3.0; E–N 2.5.

Etymology.—Latin, meaning sixth, used in reference to the toe-like inner metatarsal tubercle.

Natural history.—*E. hectus* is unusual among the species of *Eleutherodactylus* found at La Planada in that it is a diurnal species. At night individuals are found sleeping on leaves of low vegetation but during the day this is a terrestrial species and hops rapidly among the leaf litter on the forest floor and in the recesses formed by tree roots and butresses. When the frogs stop, their cryptic coloration makes them very inconspicuous. Seven juvenile females (straight, thin oviducts) were collected as well as the adult frogs. The juvenile females are 13.6–17.8 mm SVL.

Eleutherodactylus laticlavius, New Species

Figs. 3A–B

Holotype.—IND-AN 1564, an adult female, obtained at Reserva Natural

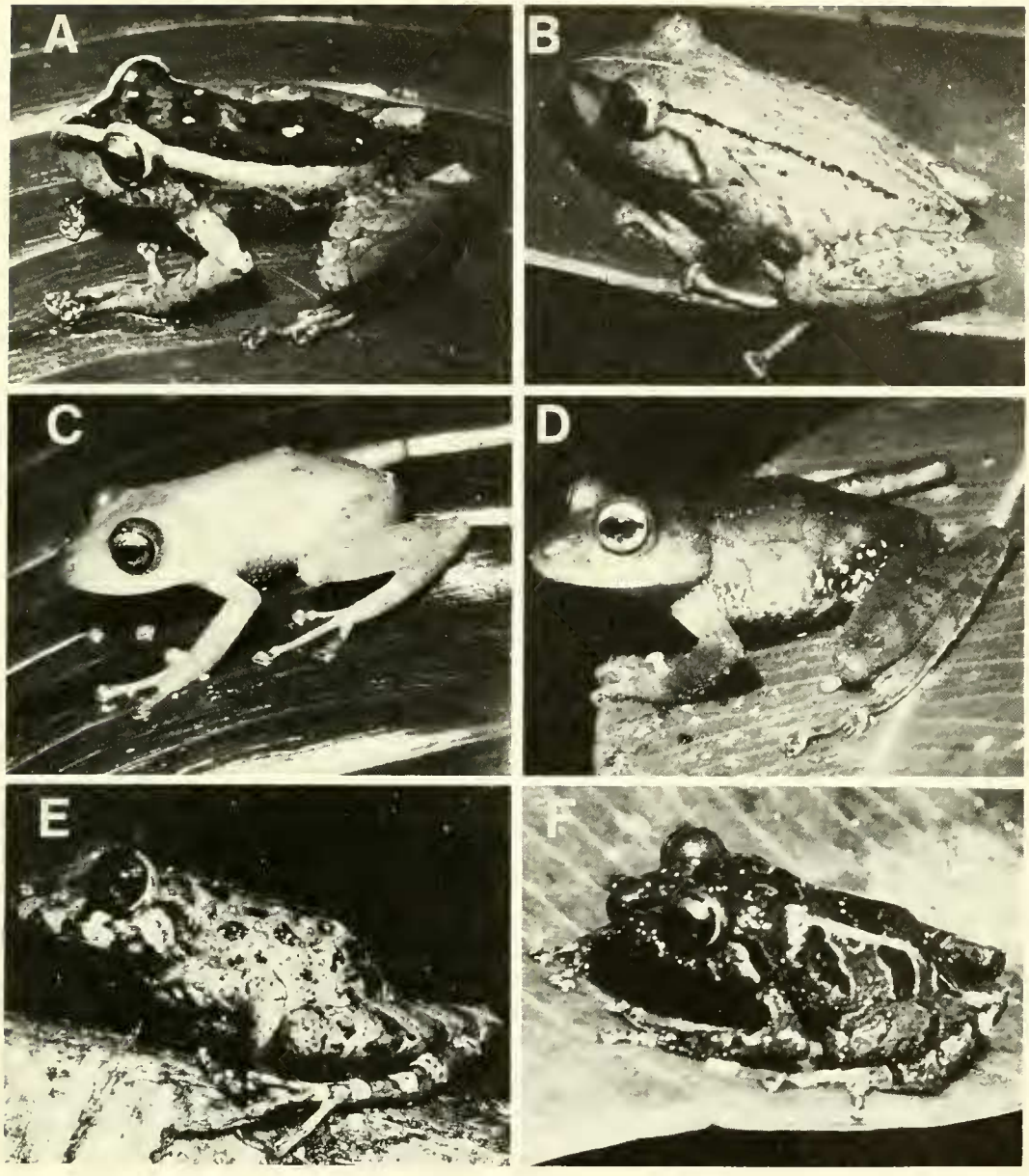

Fig. 3. *Eleutherodactylus* from La Planada. A) *E. laticlavius*, broad-band morph, IND-AN 1789, adult male, 25.3 mm SVL; B) *E. laticlavius*, thin-stripes morph, IND-AN 1480, adult female, 41.6 mm SVL; C) *E. scolodiscus*, IND-AN 1778, adult female, 22.3 mm SVL; D) *E. siopelus*, IND-AN 1811, adult female, 34.4 mm SVL; E) *E. ocellatus*, IND-AN 1441, holotype female, 45.7 mm SVL; and F) *E. verecundus*, IND-AN 1801, juvenile female, 20.1 mm SVL.

La Planada, Mcpio. de Ricaurte, Depto. Nariño, Colombia, 1780 m, on 20 June 1986 by P. A. Burrowes.

Paratypes.—IND-AN 1419, 1426, 1480, 1804, KU 212545, PAB 147, 149, 161, 163, topotypes.

Diagnosis.—1) skin of dorsum smooth with non-conical tubercles on lower back and along dorsolateral stripe, that of venter areolate; 2) tympanum distinct, higher than long, its length 25–33% eye length; 3) snout ovoid in

dorsal view, rounded in lateral profile, weakly flared in adult females; canthus rostralis distinct; 4) upper eyelid narrower than interorbital space, with small tubercle on posterior edge; no cranial crests; 5) vomerine odontophores prominent, triangular in outline; 6) males without vocal slits or nuptial pads; 7) first finger shorter than second; fingers bear broad, apically rounded pads; pads of II–IV much larger than tympanum; 8) fingers bear lateral keels; 9) no ulnar tubercles; 10) small conical tubercle on heel, short tubercle-like fold on inner edge of tarsus; 11) two metatarsal tubercles, inner oval, about 6 times size of elongate outer; many supernumerary plantar tubercles; 12) toes with lateral keels and large pads and discs (not as large as pads of outer fingers); 13) two color patterns: brown frogs with broad pale stripe from tip of snout across upper edge of eyelid and as a dorsolateral band, stripes edged with black *or* dorsum pale to dark brown with dark brown dorsolateral stripe and brown flanks; concealed surfaces of thighs brown with cream spots; facial bars and stripes and limb bars edged with cream; venter white to cream, mottled with brown; 14) adults moderate-sized, four adult males 25.3–26.3 mm SVL ($\bar{x}$ = 25.8), two adult females 39.2–41.6 mm SVL.

In general form, *E. laticlavius* resembles *E. molybrignus* Lynch but is readily distinguished from it by virtue of coloration and in having an externally visible tympanum. The pale spots on the concealed surfaces of the thighs and in the groin are creamy-white or pale yellow in life and serve to make the species quite easily recognized.

Decription.—Head as wide as body, wider than long; HW 38.0–39.5% SVL ($\bar{x}$ = 38.8, n = 4) in males, 38.9–41.8% in two females; nostrils protuberant, directed dorsolaterally; canthus rostralis distinct, edge rounded and straight or weakly sinuous; in males, E–N 84.6–87.5% eye length ($\bar{x}$ = 86.7, n = 4), in two females E–N equals eye length; loreal region concave, sloping gradually to lips; lips weakly flared (most obvious in females); upper eyelid width 71.4–100.0% IOD ($\bar{x}$ = 85.3, n = 4) in males, 66.7–91.3% in two females; tubercle on upper eyelid lies at anteriormost extent of dorsolateral fold; supratympanic fold prominent, concealing upper edge of tympanic annulus; tympanum higher than long, separated from eye by distance equal to 1 ½ to 2 times length of tympanum; in males, tympanum length 25.0–30.0% eye length ($\bar{x}$ = 27.2, n = 4), in two females 32.7%; postrictal tubercles subconical to conical; other low tubercles are evident on skin near tympanum; choanae round, small, not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly above; vomerine odontophores median and posterior to choanae, separated on midline by distance equal to an odontophore width, each bearing a transverse row of 4–6 teeth; tongue longer than wide, its posterior edge notched, posterior ⅖ not adherent to floor of mouth.

Skin of head with a few low tubercles, otherwise smooth; dorsum smooth except for non-conical tubercles along the dorsolateral line (forming a low

dorsolateral fold) and on lower back; low, non-conical tubercles on flanks and upper surfaces of limbs; anal opening not extended in sheath; discoidal folds lie well anteriad to groin; skin of throat smooth or wrinkled.

Palmar tubercle bifid, much larger than oval thenar; numerous low supernumerary palmar tubercles; subarticular tubercles small, round; lateral keels on digits not very distinct (but present); fingers with broad pads, those of II–IV wider than length of inner metatarsal tubercle, that of I small but dilated.

Small conical tubercle on heel larger than a series of small tubercles along outer edge of tarsus; toes with very slight lateral keels and round subarticular tubercles; toe pads and discs large, but not so large as those of outer fingers; when flexed hind legs are held at right angles to sagittal plane, heels narrowly overlap; heel of adpressed hind leg reaches nearly to nostril; tibia 52.8–59.3% SVL ($\bar{x}$ = 56.5, n = 4) in males, 52.2–55.4% in two females.

Coloration in preservative: Two color morphs are evident. The first has a pale cream stripe from the tip of the snout across the outer edge of the upper eyelid and then it broadens and extends posteriorly as a dorsolateral stripe (Fig. 3A). The area between the stripes is brown, edged with dark brown or black. The other morph has a narrow dark brown dorsolateral stripe, edged dorsally with cream (Fig. 3B). The dorsum between the stripes is pale to dark brown and exhibits various additional markings. The extra markings can be a simple thin cream vertebral line (IND-AN 1480), some short paravertebral stripes and spots (IND-AN 1804), or no markings (IND-AN 1426). The remaining coloration is not polymorphic and is as follows: canthal-supratympanic stripe and labial bars dark brown, edged with cream; flanks brown with some cream spots and slanted lines *or* white with brown speckling; anterior flank bears a large blotch, edged posterodorsally by thin cream line; groin dark brown with white spots or reticulation; anterior and posterior surfaces of thighs, underside of shanks, and tops of feet and tarsi dark brown/black with cream spots; bars across top of thighs black proximally, brown distally, edged with cream; shank bars brown, about widths of interspaces, oblique; inner digits white; venter white with scattered brown stippling to very densely stippled, almost a mottled brown.

In life, the striped polymorph of *E. laticlavius* is chocolate-brown above with wide yellow canthal-dorsolateral stripes. The other morph is tan dorsally with thin reddish-brown canthal-dorsolateral lines and a very thin cream-yellow middorsal line. Other coloration does not differ between morphs. The limbs are tan with brown bars edged with creamy-white; flanks and posterior surfaces of thighs yellow with brown marbling (or brown to reddish-brown with whitish blotches); venter white to tan with pink, orange, or greenish-yellow wash and brown flecks; iris golden copper with fine black reticulation and median horizontal red streak.

Measurements of holotype in mm.—SVL 39.2; tibia 21.7; HW 16.4;

head length 15.9; eyelid 3.0; IOD 4.5; tympanum length 1.7; eye length 5.2; E–N 5.2.

Etymology.—Latin, meaning having a broad stripe, and used in response to the striking pattern of one of the color morphs.

Natural history.—All adult individuals were found at night on vegetation 1.0–4.0 m above streams. Juveniles were found on low vegetation in the forest at night.

Remarks.—We consider two small (19.9–21.0 mm SVL) males as juveniles because the testes are less rotund than in the larger males. Two small females (16.2–19.9 mm SVL) have only thin straight oviducts and minute eggs.

The most common morph (broad pale stripes) is seen in three males and two females. The other morph (thin dark stripes) is seen in three males and one female.

This species may enjoy a modest distribution. We suspect that some of the cloud forest records of *E. cruentus* from western Colombia and western Ecuador that the senior author has seen (and on occasion reported) are *E. laticlavius*.

Eleutherodactylus ocellatus, New Species

Fig. 3C

Holotype.—IND-AN 1441, an adult female, obtained at Reserva Natural La Planada, Mcpio. de Ricaurte, Depto. Nariño, Colombia, 1780 m, on 3 May 1986 by P. A. Burrowes.

Paratype.—IND-AN 1460, topotype obtained 3 June 1986.

Diagnosis.—1) skin of dorsum shagreened, with scattered low, flat warts, that of venter smooth; no dorsolateral folds; 2) tympanum prominent, small, its length ⅓ eye length; 3) snout subacuminate in dorsal view, rounded in lateral profile, long; canthus rostralis prominent; 4) upper eyelid 85–105% IOD; no cranial crests; 5) vomerine odontophores large, triangular in outline; 6) males not known; 7) first finger slightly shorter than second; outer fingers bearing broad pads, tips truncate or emarginate; 8) fingers bear lateral keels; 9) small ulnar tubercles; 10) small tubercles on heel and outer edge of tarsus; short fold on inner edge of distal portion of tarsus; 11) two metatarsal tubercles, inner oval to elongate, 4 times size of round, flat outer; 12) lateral keels on toes toward bases; toe pads expanded, smaller than those of outer fingers; 13) dorsum bearing black spots with pale centers; venter cream, mottled with brown; throat cream with brown chevrons; posterior surfaces of thighs dark brown; 14) adults large, one adult female 45.7 mm SVL.

Eleutherodactylus ocellatus is most similar to *E. crenunguis* Lynch but differs in having a shorter first finger, the texture of the skin of the dorsum, and in coloration. Additionally, *E. ocellatus* is probably slightly smaller than is *E. crenunguis*.

Description.—Head as wide as body, slightly wider than long; HW 39.1–40.3% SVL; snout subacuminate but broad in dorsal view, bearing papilla at tip; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis prominent, its edge rounded and straight; snout long, E–N 101.8–103.9% eye length; loreal region concave, sloping gradually to flared lips; upper eyelid width 85.1–105.3% IOD; some low tubercles present on upper eyelid, none prominent; supratympanic fold thick, evident dorsal to tympanum; tympanum round, its length 33.3–36.4% eye length, separated from eye by distance equal to twice its length; skin of head bearing scattered low warts; choanae large, not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly above; vomerine odontophores massive, bearing a transverse row of 5–8 teeth across posterior edge, narrowly separated on midline; tongue longer than wide, its posterior edge notched, posterior ⅓ not adherent to floor of mouth.

Skin of dorsum lacking folds, shagreened but with larger, usually flat warts lying in black spots; flanks having more and more pungent warts than dorsum; anal opening not extended in sheath; transverse series of warts above vent; skin of upper surfaces of limbs essentially smooth; discoidal folds lie well anteriad to groin; skin of venter smooth or wrinkled, faint areolation (fine) evident on throat, coarse flat areolation below vent; palmar tubercle bifid, larger than elongate thenar tubercle; no supernumerary palmar tubercles (or one at base of finger III); subarticular tubercles small, round; fingers long and slender; thumb with scarcely any expansion of pad; fingers II–IV bearing broadly expanded pads, truncate or weakly emarginate at tips.

Tarsal and heel tubercles small; short fold on inner edge of tarsus just proximal to inner metatarsal tubercle (fold only half as long as tubercle); supernumerary plantar tubercles at bases of toes II (1), III (1–2), IV (2), and V (0–1); subarticular tubercles round or slightly longer than wide; toes long and slender, bearing lateral keels only on basal portions; hind limbs long; tibia 64.8–68.0% SVL; when flexed hind limbs are held at right angles to sagittal plane, heels overlap broadly; heel of adpressed hind limb extends well beyond tip of snout.

Coloration in preservative: gray-brown with large dark brown/black spots on dorsum (centers paler); limb bars narrow, oblique on shanks; dark brown patch about vent, in a brown anal triangle; dark brown bands on top of thigh, labial bars, and supratympanic stripe (no canthal stripe); posterior surfaces of thighs dark brown (or patterned with dark brown blotches, divided by invasion of cream from tops of thighs); undersides of limbs brown with cream blotches; venter cream with dense brown spotting and marbling; throat cream with brown chevrons, ending in the mottling on the chest.

In life, *E. ocellatus* was grayish-tan with brown ocelli surrounding tan tubercles; limbs grayish-tan with brown transverse bars; venter creamy tan with brown marbling; brown chevrons were visible on the throats of larger individuals; iris brown with gray blotches.

Measurements of holotype in mm.—SVL 45.7; tibia 31.1; HW 18.4; head length 18.6; upper eyelid 4.0; IOD 4.7; tympanum 2.0; eye 5.5; E–N 5.6.

Etymology.—Latin, in reference to the presence of ocelli on the dorsum.

Natural history.—Individuals were active at night and were found sitting on vegetation (0.5–2.0 m above ground) above stream banks or on branches high in the tree canopy.

Remarks.—Only two specimens were used to prepare the description but natural history data and some color data are available for other specimens left in the reference collection at the Reserva Natural.

Tentatively, we consider *E. ocellatus* most closely related to *E. crenunguis* although it could be viewed as equally close to *E. rubicundus* (Jimenez de la Espada).

Eleutherodactylus scolodiscus, New Species

Figs. 2B, 3D

Holotype.—IND-AN 1416, an adult female, obtained at Reserva Natural La Planada, Mcpio. de Ricaurte, Depto. Nariño, Colombia, 1780 m, on 2 May 1986 by P. A. Burrowes.

Paratypes.—IND-AN 1417–21, 1473, KU 212546–48, PAB 158, 169, topotypes.

Diagnosis.—1) skin of dorsum shagreened, that of venter areolate; no dorsolateral folds; 2) tympanum round, not prominent, about ⅓ eye length; 3) snout subacuminate in dorsal view, rounded in lateral profile, with papilla at tip; canthus rostralis moderately sharp; 4) upper eyelid narrower than interorbital space; no cranial crests; 5) vomerine odontophores absent or only barely evident; 6) males with long vocal slits but lacking nuptial pads; 7) first finger shorter than second; pads of outer fingers dilated, that of III bearing papilla at tip; 8) fleshy keel on fingers II–IV; 9) no ulnar tubercles; 10) minute tubercle on heel, none on tarsus; 11) two metatarsal tubercles, inner oval, 5 times size of round outer; many supernumerary plantar tubercles; 12) toes with fleshy fringe and large digital pads; toes II–IV bearing papillae at tips; 13) body lacking pattern except for pale areas on concealed surfaces of thighs, groin, and axilla (orange in life); 14) adults small, males 17.9–20.4 mm SVL ($\bar{x}$ = 19.6 ± 0.3, n = 7), females 20.1–22.3 mm SVL ($\bar{x}$ = 21.4, n = 4).

Eleutherodactylus scolodiscus is considered a member of a small group of species having papillae at the digital tips (*E. chalceus*, *E. gularis* [Boulenger], and *E. vocator* Taylor). This group of species may be a part of the *diastema* species group, long recognized for Middle America, but until evidence is provided that the species having simple digits (*E. diastema* [Cope] and *E. hylaeformis* [Cope]) share some explicit character with those species having papillose digits, we will not recognize the species group. *Eleutherodactylus scolodiscus* differs from *E. chalceus* and *E. gularis* in having smaller (shorter)

papillae on the digital tips and in having orange areas on the concealed surfaces of the limbs. The papillae of *E. scolodiscus* are larger than are those of *E. vocator*, whose digital pads are often described as pointed (Taylor, 1955). *Eleutherodactylus vocator* is a much smaller frog and is more densely pigmented than is *E. scolodiscus*.

Description.—Head large, usually wider than body, usually longer than wide; HW 37.1–40.4% SVL ($\bar{x}$ = 38.8 ± 0.4, n = 7) in males, 38.0–41.2% ($\bar{x}$ = 39.8, n = 4) in females; nostrils protuberant, directed laterally; canthus rostralis concave; loreal region concave, sloping abruptly to lips; lips not flared; snout long, E–N 79.3–89.7% eye length ($\bar{x}$ = 83.8 ± 1.6, n = 7) in males, 86.2–93.3% ($\bar{x}$ = 90.5, n = 4) in females; upper eyelid width 76.0–95.7% IOD ($\bar{x}$ = 84.8 ± 2.8, n = 7) in males, 72.0–92.0% ($\bar{x}$ = 79.3, n = 4) in females; upper eyelid bearing small tubercles; supratympanic fold low, concealing uppermost edge of tympanum; tympanum round, not prominent, separated from eye by distance about equal to its own diameter; tympanum length 22.6–31.0% eye length ($\bar{x}$ = 26.7 ± 1.1, n = 7) in males, 29.6–34.5% ($\bar{x}$ = 31.9, n = 4) in females; postrictal tubercles subconical; choanae large, not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly above; vomerine odontophores absent, or if some evidence of structures exist, they are very slight, slanted structures median and posterior to choanae; no vomerine teeth; tongue large, slightly longer than wide, posterior edge notched, posterior ⅔ not adherent to floor of mouth; long vocal slits posterolateral to tongue in males.

Skin of flanks areolate; anal opening not extended in sheath; discoidal folds present; forelimb slender; palmar tubercle bifid, larger than oval thenar; subarticular tubercles round; fleshy fringe present on at least fingers II–IV; some evidence of fleshy fringe along outer edge of palm as well; digital discs broad; pad of thumb scarcely dilated, those on fingers II–IV dilated; pad of finger III bearing short papilla at tip (in some individuals, there is a hint of a similar structure on IV); digital pads of fingers II–IV feebly pointed; subarticular tubercles of feet low, round; fleshy fringe along edges of toes; digital pads of toes II–IV with pointed tips (short papillae, Fig. 2B); hind limbs short, tibia 48.0–51.5% SVL ($\bar{x}$ = 49.4 ± 0.5, n = 7) in males, 47.1–53.3% ($\bar{x}$ = 51.2, n = 4) in females.

Coloration in preservative: dorsally, cream with fine black punctations, clumped in various places and forming suggestions of dorsal markings (vague limb bars, band on forelimb, sacral chevron, occipital W, loose vermiculation on dorsum) in some individuals; white transverse bar anteriad to vent, edged with black punctations; venter less densely punctated; clear patches on posterior surfaces of thighs, anterior surfaces of thighs, groin, and axillae.

In life, *E. scolodiscus* was very pale tan above with a pink or orange suffusion; some individuals also had brown specks on the dorsum; limbs tan with brown flecks sometimes forming light transverse bands; groin and posterior

surfaces of thighs orange; venter white without dark specks; iris pale (but bright) blue with fine black reticulations.

Measurements of holotype in mm.—SVL 20.1; tibia 10.6; HW 8.0; head length 8.4; eyelid width 1.8; IOD 2.5; tympanum 0.8; eye length 2.7; E–N 2.5.

Etymology.—The specific name is Greek (*skolos*, pointed, + *diskus*, digital disc) and refers to the shape of the digital pad of this species.

Natural history.—*E. scolodiscus* was found at night sitting on leaves or mossy branches 1.0–3.0 m above the ground in dense forest or on vegetation along closed-canopy streams.

Remarks.—Initially, we had confused this species with *E. parvillus* Lynch but the two are readily distinguished based on digital morphology and the condition of the vomerine odontophores. The report of *E. parvillus* from Depto. Cauca by Lynch and Ruiz (1983) does not apply to *E. scolodiscus*.

Eleutherodactylus siopelus, New Species
Fig. 3E

Holotype.—IND-AN 1563, an adult female obtained at Reserva Natural La Planada, Mcpio. de Ricaurte, Depto. Nariño, Colombia, 1780 m, on 20 June 1986 by P. A. Burrowes.

Paratypes.—IND-AN 1413–15, 1423–25, 1431, 1482, 1562, 1812–14, 1819–20, 1822, KU 212551–53, topotypes.

Diagnosis.—1) skin of dorsum shagreened, that of venter areolate; short dorsolateral folds present; 2) tympanum absent; 3) snout subacuminate in dorsal view, rounded in lateral profile, with papilla at tip; canthus rostralis sharp; 4) upper eyelid narrower than IOD; low cranial crests present; 5) vomerine odontophores prominent, triangular in outline; 6) males lack vocal sac and slits; no nuptial pads; 7) first finger shorter than second; digital pads large; 8) fingers with fleshy fringe; 9) row of conical ulnar tubercles; 10) heel bearing calcar; row of tubercles along outer edge of tarsus, low fold on distal fourth of inner edge of tarsus; 11) two metatarsal tubercles, inner oval, 3 times size of flat outer; numerous supernumerary plantar tubercles; 12) toes with fleshy fringes, toe pads slightly larger than those of outer fingers; 13) dorsum brown with darker markings, venter white with brown flecks; posterior surfaces of thighs dark brown with cream flecks (most have a series of white spots across upper edge of posterior thigh surface); 14) adults moderate-sized, males 18.6–27.3 mm SVL ($\bar{x} = 23.7 \pm 0.7$, $n = 14$), females 34.3–40.0 mm SVL ($\bar{x} = 37.4$, $n = 4$).

We are quite uncertain of the relationships of *E. siopelus* but tentatively associate it with *E. acatallelus* Lynch and Ruiz from which it is easily distinguished in lacking the tympanum. The absence of a tympanum is uncommon in *Eleutherodactylus* but nearly a dozen species are known to lack these structures. At present, no other species lacking a tympanum has

prominent heel calcars. In physiognomy and general distribution of warts, *E. siopelus* resembles *E. quinquagesimus* but lacks the transverse interorbital fold (and of course is distinguished based on ear morphology).

Description.—Head as broad as body, wider than long; HW in males 38.7–44.9% SVL ($\bar{x}$ = 40.7 ± 0.5, n = 14), in females 40.9–43.6% ($\bar{x}$ = 42.8, n = 4); nostrils scarcely protuberant, directed dorsolaterally; canthus rostralis sharp, very slightly concave; tip of snout not concave as in *E. quinquagesimus*; upper eyelid width 75.9–108.7% IOD ($\bar{x}$ = 92.2 ± 2.4, n = 14) in males, 83.3–85.4% ($\bar{x}$ = 84.8, n = 4) in females; small tubercle on upper eyelid at anterior extent of dorsolateral folds (which extend onto posterolateral part of eyelid); loreal region slightly concave, sloping abruptly to lips; lips not flared; snout long, E–N 81.1–100.0% eye length ($\bar{x}$ = 90.1 ± 1.9, n = 14) in males, 96.0–102.2% ($\bar{x}$ = 99.5, n = 4) in females; supratympanic fold evident, short, bordered ventrally by a number of conical to subconical tubercles, postrictal largest; a few non-pungent tubercles on face between nostril and rictus; skin of head finely shagreened; choanae small, not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly above; vomerine odontophores median and posterior to choanae, separated medially by distance equal to ½ – ⅔ an odontophore width, bearing 3–7 teeth in a curved row across posterior edge; tongue longer than wide, its posterior border not notched, posterior ¼ – ½ not adherent to floor of mouth.

Skin of dorsum shagreened, becoming slightly coarser on lower back; doroslateral folds reaching posteriorly to about level of sacrum; skin on flanks more coarsely tuberculate than on lower back; skin on upper surfaces of limbs bearing enlarged tubercles and short ridges; anal opening not extended in sheath; discoidal folds evident on lower belly; row of conical ulnar tubercles extending onto outer edge of palm; palmar tubercle bifid, about same size as oval thenar; palm bearing numerous supernumerary tubercles; subarticular tubercles round, non-conical; fingers III–IV bearing broad pads (and discs), about twice width of digit below pad; pad of finger II about 1 ½ times digit width, that of thumb only slightly wider than digit; if digits are equally adpressed, tip of I reaches about half way up disc of II.

Tubercles on outer edge of tarsus about ¼ size of calcar; fold evident along outer edge of sole, bearing low tubercles; subarticular tubercles round (except for basal tubercles of toes III–IV, longer than wide); when flexed hind legs are held at right angles to sagittal plane, heels overlap; heel of adpressed hind leg reaches to level of snout tip; shank 55.2–70.3% SVL ($\bar{x}$ = 64.6 ± 1.0, n = 14) in males, 59.0–64.8% ($\bar{x}$ = 61.6, n = 4) in females.

Coloration in preservative: dorsum brown with darker interorbital bar, occipital W, sacral chevron, and limb bars; facial markings vague; lower flanks mottled with cream (white); venter white with brown flecks, throat more heavily peppered with brown; undersides of limbs brown with cream patches; posterior surfaces of thighs dark brown with minute cream flecks in

males; in females, upper edge of dark brown patch on posterior surfaces of thighs contains a series of white spots; evident; in larger females, flanks have very dark edging to white blotches and spots.

In life, *E. siopelus* was uniform chocolate-brown or tan above with brown chevrons and limb bars; flanks brown with varying degrees of white mottling (Fig. 3E); posterior surfaces of thighs brown with small white flecks in females (brown in males); venter white with brown blotches; iris golden yellow.

Measurements of holotype in mm.—SVL 38.6; tibia 23.0; HW 16.7; head length 15.5; upper eyelid width 3.5; IOD 4.1; eye length 5.0; E–N 5.0.

Etymology.—Greek, meaning silent, in reference to the absence of vocal apparatus and ear (the species probably does not call).

Natural history.—*E. siopelus* was found only at night, when it was abundant on vegetation (0.5–2.0 m above ground) overhanging streams. The only immature individual obtained is a juvenile or young female (thin oviducts with a few bends) 31.1 mm SVL (IND-AN 1482).

Remarks.—Savage (1987) has made extensive use of the disposition of the fibers of the *m. depressor mandibulae* in order to characterize various lineages of eleutherodactyline frogs. While he does use other traits as well, we are skeptical of the use of this muscle until some homologies are established. In *E. siopelus*, the fibers of the *m. depressor mandibulae* insert upon the ventral edge of the cristae paroticae (ca. 90% of the fibers) and upon the fascia of the shoulder. There are no fibers inserting on the ventral process of the squamosal nor, obviously, on the tympanic annulus. While there is an obvious difference in fiber lengths (those inserting on the cristae paroticae are shorter than those extending onto the fascia of the shoulder), we do not treat these as separate slips. The peculiar depressor formula that is generated from this distribution (dfSQ, if one sees two slips because there are two insertional sites, or dfsq) is otherwise known in a species group (also considered by some as the genus *Hylactophryne*) of the subgenus *Craugastor* of *Eleutherodactylus* (Savage, 1987:42).

Eleutherodactylus sulculus, New Species

Holotype.—IND-AN 1481, an adult female obtained at Reserva Natural La Planada, Mcpio. de Ricaurte, Depto. Nariño, Colombia, 1780 m, on 4 June 1986 by P. A. Burrowes.

Paratypes.—IND-AN 1537, 1557, 1815, topotypes.

Diagnosis.—1) skin of dorsum bearing many small tubercles, almost shagreened, that of venter areolate; traces of dorsolateral folds at region of sacrum; 2) tympanum prominent, its length ⅓ – ½ eye length; 3) snout ovoid in dorsal view, rounded in lateral profile; canthus rostralis sharp; 4) IOD greater than upper eyelid width; cranial crests present; 5) vomerine odonto-

phores prominent, subtriangular in outline; 6) males lack vocal slits; males with white nuptial pad on thumb; 7) first finger shorter than second; fingers II–IV with large discs and pads; 8) fingers with lateral fringes; 9) no enlarged ulnar tubercles; 10) no enlarged tubercles on heel or tarsus; low fold on distal end of inner edge of tarsus; 11) two metatarsal tubercles, inner oval, 6 times size of subconical outer; supernumerary plantar tubercles at bases of each toe; 12) toes bearing lateral fringes, large digital pads, as large as those of hand; 13) dorsum brown with darker flanks; venter cream with brown spots or reticulum; posterior surfaces of thighs brown; 14) adults moderate sized, one adult male 26.3 mm SVL, one adult female 43.0 mm SVL.

Eleutherodactylus sulculus is a drab frog with little of note to readily distinguish it from the many other species of the genus. The presence of cranial crests in conjunction with a prominent tympanum and the brown coloration serve to separate the species from named taxa. Tentatively, we associate it with *E. supernatis* Lynch from which it is readily distinguished based on coloration and the longer limbs.

Description.—Head as broad as body, broader than long; HW 38.4–40.4% SVL; nostrils protuberant, directed dorsolaterally; canthus rostralis straight; loreal region scarcely concave, sloping abruptly to lip; lips not flared; upper eyelid width 65.2–90.3% IOD, bearing only low, flat tubercles; edges of frontoparietals upturned, forming low cranial crests; low supratympanic fold, obscured by low flat tubercles in temporal region; tympanum higher than long, dorsal and posterodorsal edges concealed, separated from eye by distance equal 1 ½ times length of tympanum; tympanum length 33.3–48.0% eye length; many low flat tubercles anterior to tympanum; postrictal tubercles subconical; choanae small, round, not concealed by palatal shelf when roof of mouth is viewed from directly above; vomerine odontophores median and posterior to choanae, separated on midline by a distance equal to an odontophore width, each odontophore up to 3–5 times size of a choana (in largest individual), each with a row of 3–5 teeth across posterior edge of odontophore; tongue longer than wide, its posterior edge notched, posterior ⅖ not adherent to floor of mouth.

Skin of dorsum bearing many low, small tubercles, more coarse on flanks; discoidal folds well anterior to groin; anal opening not extended in sheath; minute antebrachial tubercle present (no other ulnar tubercles); palmar tubercle divided, inner tubercle larger; thenar tubercle oval, larger than largest palmar tubercle; numerous supernumerary palmar tubercles; subarticular tubercles round; lateral keel along outside of palm extending onto lateral surface of finger IV; pads of fingers II–IV larger than tympanum (also wider than length of inner metatarsal tubercle).

Low tubercles on heel, outer edge of tarsus; low fold on inner edge of tarsus, just proximal to inner metatarsal tubercle; subarticular tubercles round, smaller than those of hand; when flexed hind legs are held at right

angles to sagittal plane, heels overlap; heel of adpressed hind limb reaches anterior to eye or to nostril; shank 53.7–60.4% SVL.

Coloration in preservative: dorsum pale to dark brown with darker flanks; flanks obliquely barred; limb bars narrow, those on shanks transverse or slightly oblique; undersides of limbs brown; throat more or less densely mottled with brown over cream ground color; venter cream with brown flecks, spots, and reticulation; groin and concealed surfaces of limbs brown.

In life, *E. sulculus* was tan, brown, or reddish-brown above with darker brown markings; venter creamy-white with brown mottling; posterior surfaces of thighs brown with creamy-white mottling; iris bronze-brown with golden outer rim.

Measurements of holotype in mm.—SVL 43.0; shank 23.1; HW 17.0; head length 17.4; upper eyelid width 3.9; IOD 5.4; tympanum length 2.4; eye length 5.0; E–N 5.0.

Etymology.—The diminutive of the Latin *sulcus*, a furrow, in reference to the low furrow created by the cranial crests.

Natural history.—Individuals were found on vegetation (1–2 ½ m above ground) overhanging streams or in the tree canopy. So few individuals were secured of this species that we cannot accurately judge its size. Two juvenile females (thin oviducts) are 21.0 and 32.2 mm SVL. Because this species is so uncommon at La Planada we suspect that it occurs there at either the lower or upper altitudinal limit of its distribution.

Eleutherodactylus verecundus, New Species

Fig. 3F

Holotype.—IND-AN 1834, an adult female, obtained at Reserva Natural La Planada, Mcpio. de Ricaurte, Depto. Nariño, Colombia, 1780 m, on 26 April 1986 by P. A. Burrowes.

Paratypes.—IND-AN 1457, 1492, 1801, KU 212549–50, PAB 176, topotypes.

Diagnosis.—1) skin of dorsum bearing low flat warts, that of venter areolate; partial dorsolateral folds present; 2) tympanum round, obscure, its length ⅕ – ⅓ eye length; 3) snout subacuminate in dorsal view, rounded to nearly spatulate in lateral profile; canthus rostralis round; 4) upper eyelid narrower than IOD; no cranial crests; 5) vomerine odontophores prominent; 6) males with vocal slits but no nuptial pads; 7) first finger shorter than second; digital pads large, round; 8) fingers with lateral keels; 9) two ulnar tubercles; 10) conical tubercle on heel; row of small tubercles along outer edge of tarsus; short fold on inner edge of tarsus; 11) two metatarsal tubercles, inner oval, twice size of round outer; numerous small supernumerary plantar tubercles; 12) toes with lateral fringes; toe pads large, but smaller than those of outer fingers; 13) dorsum brown with pale dorsolateral stripes and brown blotches; venter brown with darker spots; throat of females with brown

chevrons; posterior surfaces of thighs thrown with cream flecks; 14) adults small, four males 18.0–21.9 mm SVL ($\bar{x}$ = 20.2), two females 22.4–22.5 mm SVL.

Eleutherodactylus verecundus superficially resembles a series of small species found in the upper Amazon Basin (e.g., *E. carvalhoi* Lutz and Kloss, *E. croceoinguinis* Lynch, and *E. martiae* Lynch) but is easily distinguished from each by virtue of its larger tympanum (which is faintly visible externally and only partially concealed), prominent vomerine odontophores, and ventral color pattern. We suspect that *E. verecundus* is closely related to *E. cabrerai* Cochran and Goin; that species is larger, has longer hind legs, has a longer snout, less prominent vomerine odontophores, and a concealed tympanum.

Description.—Head as wide as body, longer than wide; HW 35.6–38.0% SVL ($\bar{x}$ = 36.4, n = 4) in males, 35.7–40.0% in two females; nostrils protuberant, directed laterally; canthus rostralis rounded, but evident, concave; loreal region concave, sloping gradually to lips; E–N 75.0–92.9% eye length ($\bar{x}$ = 86.7, n = 4) in males, 93.1–94.6% in two females; upper eyelid tuberculate, its width 85.0–106.7% IOD ($\bar{x}$ = 96.6, n = 4) in males, 78.3–90.0% in two females; tympanum superficial but difficult to see (partially concealed beneath thin skin on side of head), round, its length 21.4–32.1% eye length ($\bar{x}$ = 26.5, n = 4) in males, 24.3–27.6% in two females; supratympanic fold thick; postrictal tubercles large, subconical; skin of top of head with low tubercles, that of throat of females areolate; choanae small, not concealed by palatal shelf of maxiallary arch when roof of mouth is viewed from directly above; vomerine odontophores median and posterior to choanae, about the size of a choana (or slightly larger), subtriangular in outline, prominent, separated on midline by a distance equal ½ width of an odontophore, bearing 3–4 teeth in a transverse row; tongue longer than wide, its posterior edge not notched, posterior ⅔ not adherent to floor of mouth; short vocal slits posterolateral to tongue in males; vocal sac single, subgular.

Skin of dorsum bearing low, flat warts which provide some suggestion of partial dorsolateral folds (accentuated by pale stripes) from scapular region to slightly beyond sacral region; flanks and upper surfaces of limbs bear low tubercles; discoidal folds well anteriad to groin; two large ulnar tubercles; outer edge of palm bearing row of subconical tubercles; palmar tubercle bifid, smaller than oval thenar tubercle; low supernumerary palmar tubercles present; subarticular tubercles round, low; pad of thumb much smaller than those of other fingers (of II about size of tympanum; of III–IV much larger than tympanum).

Low fleshy keel along distal ⅓ of inner edge of tarsus; inner metatarsal tubercle twice as long as wide; subarticular tubercles round, not prominent; tubercles along lateral edge of sole; when flexed limbs are held at right angles to sagittal plane, heels just overlap; heel of adpressed hind limb reaches just anterior to eye; shank 47.8–51.4% SVL ($\bar{x}$ = 49.1, n = 4) in males, 48.7–49.8% in two females.

Coloration in preservative: dorsum brown with pale dorsolateral stripes (in mid-region of body only) and dark brown blotches edged with cream halos (interorbital bar, scapular chevrons, sacral blotch, suprainguinal spots); limb bars narrow, often not crossing limb; anal patch dark brown; slanted bars (or rows of spots) on flanks; facial markings dark brown, consisting of canthal blotch, two lip bars, and postocular stripe (latter bordered ventrally by cream band on postrictal tubercles); groin and posterior surfaces of thighs brown with cream flecks; venter brown with darker spots; in females, dark spotting on venter forms a pattern of chevrons (edged with cream) on throat; in males, throat brown except for dark spots along edges of lips.

In life, *E. verecundus* is brown above with darker brown markings; dorsolateral stripes cream or orange, bearing small cream or orange tubercles; postrictal tubercles orange; limbs brown with dark brown transverse bars; toes orange with brown pads; venter tan or brown with brown or reddish-brown flecks; iris bright copper-orange.

Measurements of holotype in mm.—SVL 22.5; shank 11.2; HW 9.0; head length 9.3; upper eyelid width 1.8; IOD 2.0; tympanum length 0.9; eye length 3.7; E–N 3.5.

Etymology.—Latin, meaning bashful or shy, and used in the sense that this species has no striking feature in its color pattern or coloration.

Natural history.—*E. verecundus* is nocturnal. Individuals were found sitting on leaves 0.3–1.5 m above the ground in the forest and along stream banks. One individual was found sitting on a steep dirt bank behind a small cascade.

Our sample is small but we are impressed by the slight sexual dimorphism in size evident (in most species of the genus, females are about 140% the size of males whereas in this species the two females are only 111% the size of males. A single immature female is available (IND-AN 1801); the frog has straight, simple oviducts and is 20.1 mm SVL.

DISCUSSION

The point of this paper is to describe the new species and to report records of other species from the Reserva Natural La Planada. However, we also wish to point out that some habitat segregation is evident in this very large eleutherodactyline fauna (Table 1).

Two species are terrestrial. One of these (*E. hectus*) is the only diurnal eleutherodactyline frog in the fauna. The other terrestrial species (*E. babax*) is nocturnal as are all other species of the *discoidalis* "group." Although the Reserva is cloud forest, there are small pastures within the reserve. Additionally, the habitat along the road leading into the Reserva is cut-over and disturbed. In these habitats one finds only *E. achatinus*, a species not found within forested habitats. Three species are very closely associated with

streams, living among the rocks and crevices within the stream (*E. anatipes*, *E. duellmani*, and *E. loustes*). There are substantial size differences among these three species; in addition, they may be segregated altitudinally in that *E. anatipes* and *E. loustes* occur at lower elevations both at La Planada and elsewhere than does *E. duellmani*.

The other 12 species taken (all from the 1780 m site) were found on vegetation in the forest at night. In two cases (*E. celator* and *E. eremitus*), daytime collecting revealed that the frogs use bromeliads as retreats; at night, neither species explicitly was associated with bromeliads (which were everywhere abundant within the forested facies). For five species (*E. laticlavius*, *E. ocellatus*, *E. siopelus*, *E. sulculus*, and *E. verecundus*), there was a clear association with vegetation overhanging the abundant streams on the plateau forming the bulk of the Reserva. At most cloud forest localities with which the senior author is familiar, *E. w-nigrum* is a clear associate of forested streams but at La Planada, the junior author noted no such association (however, she mostly captured juvenile and subadult individuals). As noted in the species accounts, the activity of *E. appendiculatus* noted by the junior author (diurnal, on forest vegetation) is at variance with observations on the species in Ecuador (Miyata, 1980) where the senior author also found the animals to be nocturnal. However, so few individuals of this species were taken, and appear to be immatures, that we are reluctant to suggest that her observations require revision of Miyata's (1980) summary.

Data on vertical distribution within the forest were not taken except incidentally. Some species, normally found at modest heights in the forest, were found in the tree canopy. There are too few data points for us to suggest that these observations mean more than these eleutherodactyline frogs probably are active on vegetation anywhere from a few centimeters above the forest floor to areas 6–7 m high; most of the frogs were collected within 2 m of the forest floor, a value coincident with the normal reach of the junior author.

These observations provide little evidence of habitat partitioning along axes of time and microhabitat (Table 1). No data were collected relative to foods of these frogs but we suspect that there is limited partitioning based on prey type or prey size (our suspicion is based on published work by Duellman, 1978, for another fauna, and the senior author's preliminary study of material from several sites in western Ecuador). These eleutherodactyline frogs *may* compete along these three dimensions but if they do, the distinctions are so slight as to be overlooked during a 3 month field study.

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Naturales (INDERENA), assisted the study by providing export permits and loaning the specimens for study abroad.

SUMMARY

The eleutherodactyline frog fauna at La Planada, a biological reserve in the cloud forests of southwestern Colombia, consists of at least 19 species. Eight of these are described here as new species. Two of the 19 species were found at lower elevations (ca. 1200–1250 m) at the lower limits of the Reserva Natural La Planada whereas the other 17 species were found on the forested plateau at 1780 m. Gross ecological segregation within the fauna is minimal. One species is a diurnal frog and is terrestrial. Another is terrestrial but nocturnal. One species is restricted to pastures within the forested region. Three species are confined to microhabitats essentially within streams. One species is found only in pastures and other cleared areas. The other 12 species co-occur ecologically.

RESUMEN

La fauna de ranas del género *Eleutherodactylus* de La Planada, una reserva biológica en los bosques nublados del sur-oeste de Colombia, incluye por lo menos 19 especies. Ocho de ellas se describen como especies nuevas. Dos de las 19 especies se encuentran en los limites más bajos de la reserva (ca. 1200–1250 m), pero la mayoria (17 especies) se encuentran en la mesata forestada a los 1780 m. En general, las diferencias ecológicas entre las especies son minimas. Una de las especies es terrestre y diurna, mientras otra es terrestre y nocturna. Una especie se encuentra únicamente en los potreros, y tres especies estan limitadas a microhabitats asociados a quebradas. Las otras 12 especies se encuentran simultáneamente en habitats similares dentro del bosque.

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